Ann. Natal Mus. Vol. 39 Pages 165–183 Pietermaritzburg December, 1998

A new Namibian wormlion species, with an account of the biogeography of *Leptynoma* Westwood *s. str.* and its association with anthophily in the Fynbos and Succulent Karoo Biomes (Diptera, Vermileonidae)

by

B. R. Stuckenberg
(Natal Museum, P. Bag 9070, Pietermaritzburg 3200, South Africa;
e-mail: bstucken@nmsa.org.za)

ABSTRACT

The significance of the Gariep Centre of Endemicity is noted; this region includes the Richtersveld south of the Orange River in north-western South Africa and the adjacent parts of southern Namibia, where a rich succulent flora exists. A small but distinctive fauna of vermileonid flies is endemic in the Gariep. The new species and member of the Gariep fauna, *Leptynoma* (*Leptynoma*) *kirkspriggsi* sp. n., is described from southern Namibia. New records are given of vermileonid species in western South Africa. Cladistic analysis of *Leptynoma* Westwood *s. str.* reveals a basal dichotomy, with *L. sericea* Westwood as sister-species of the other four which form a stepwise clade, with *L. appendiculata* (Bezzi) basal to *L. hessei* (Stuckenberg), *L. namaquaensis* (Stuckenberg) and *L. kirkspriggsi* sp. n. The two older species (*sericea* and *appendiculata*) inhabit the Fynbos Biome, whereas the three younger species occur in the Succulent Karoo Biome.

The distribution of *Leptynoma s. str.* is mapped and its biogeography discussed. Cladogenesis accords with botanical evidence that Fynbos is the older biome and Succulent Karoo a younger biome with many fynbos affinities. It is proposed that the constraints limiting the distribution of these vermileonids relate to selective anthophily and nectarivory, for which the flies show strong morphological adaptations. Studies by other workers are cited, of guild associations between fynbos plant taxa and large species of Nemestrinidae and Tabanidae with an extremely long proboscis. Several striking examples are cited of mouthpart elongation for nectarivory in fynbos representatives of other, unrelated families of Diptera. Less extreme cases of labial elongation often occur among fynbos flies. Cladogenesis in the Succulent Karoo would have been coeval with the evolution of that biome in response to extreme summer aridity which began to develop in the Pliocene.

INTRODUCTION

A region of great biological interest is the mountainous Richtersveld, enclosed by the large northward bend in the course of the Orange River before it enters the sea in north-western South Africa (Fig. 1). This arid, spectacular terrain is renowned botanically for its wealth of endemic succulents (Williamson 1990;, Hilton-Taylor 1994). Its northern border is the Orange River, but this is a geographical artefact without biological significance. Similarly arid, highly broken topography with an extension of the same rich succulent flora, lies to the north of the river in southern Namibia. The Huns Mountains and the Huib Mountains with their western outliers overlooking the southern section of the Namib Desert, comprise, with the Richtersveld and northern fringes of Namaqualand, a complex biogeographical entity. As a centre of endemicity, called the Gariep, it is known to Botanists (see below) but seems to have attracted scant notice from Entomologists.

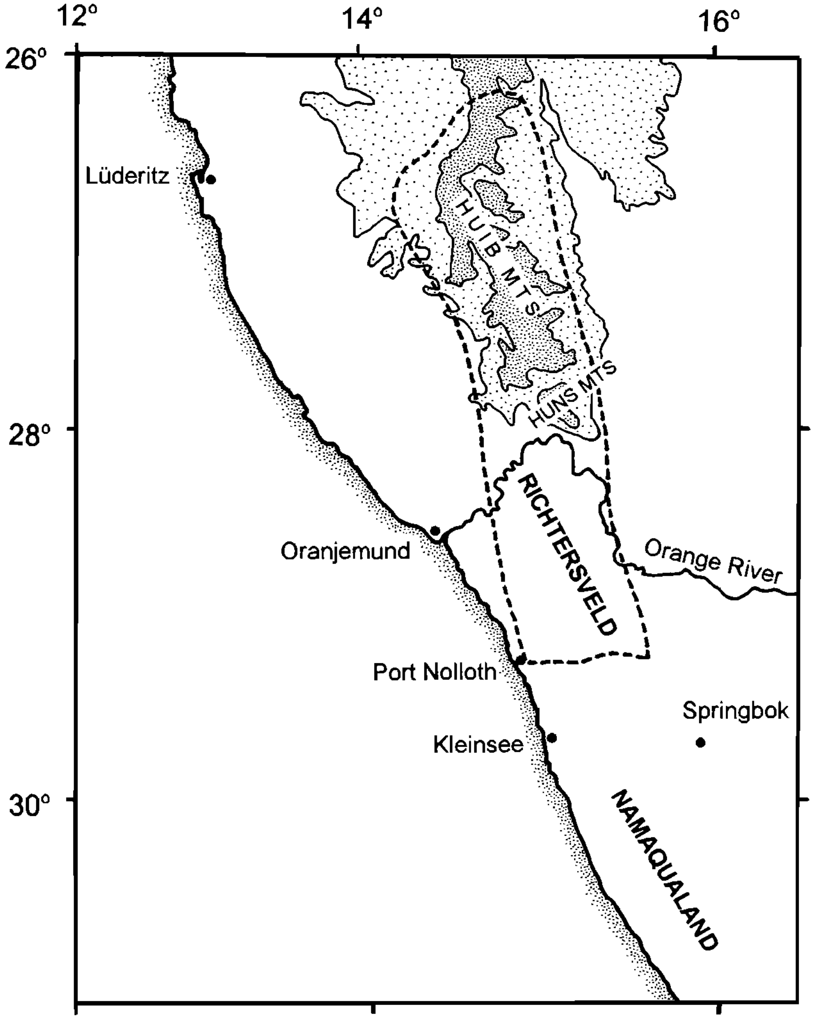

12°
14°
16°
26°
28°
30°
Lüderitz
HUIB MTS
HUNS MTS
RICHTERSVELD
Oranjemund
Orange River
Port Nolloth
Springbok
Kleinsee
NAMAQUALAND

Fig. 1. Map showing the location of the Gariep Centre of Endemicity (enclosed by broken line). (After Hilton-Taylor 1994.)

Discoveries in recent years have revealed the presence of a distinctive fauna of the palaeoendemic family Vermileonidae in the Gariep Centre. *Vermilynx vansoni* (Stuckenberg) was found first in the Richtersveld (Stuckenberg 1965), and is now known from Rosh Pinah district in southern Namibia (Stuckenberg 1995*a*). *Leptynoma* (*Perianthomyia*) *phantasma* Stuckenberg (1996*b*) was described from a site near the desolate Aurusberg mountains northwest of Rosh Pinah. A collection of vermileonids made recently by staff of the National Museum of Namibia now extends knowledge of this fauna. Its source is the Rooiberg mountain, and it contains three species: *V. vansoni*, *L.* (*P.*) *phantasma*, and a new species of *Leptynoma s. str.* This is the only record worldwide of three vermileonid species occurring sympatrically.

Another collection of vermileonid flies, made in 1996 during an expedition led by Dr M. E. Irwin of the University of Illinois, was provided by Dr D. W. Webb. This fresh material enables me to supplement the definition of *Leptynoma s. str.* and adds new distribution records.

The objectives of the present study are as follows: to describe the new Namibian species and establish its relationships, to augment the definition of *Leptynoma s. str.* and improve the key to species, to list new records, and to map the distribution of the species and relate this to plant biomes and centres of endemicity.

MATERIAL AND METHODS

The material consists of pinned flies from the National Museum of Namibia, Windhoek (NMNW); the Natal Museum (NMSA); the South African Museum, Cape Town (SAMC); and the Center for Biodiversity, Illinois Natural History Survey, Champaign (INHS). Methods used and morphological terminology follow previous publications (Stuckenberg 1996b, 1998). Elongation of the proboscis is expressed through a ratio obtained by dividing the length of the proboscis by the length of the mesonotum. Label data are cited as in the original; a slash (/) indicates the end of a line of print, two slashes (//) signify data on a second label, and supplementary information is given in square brackets.

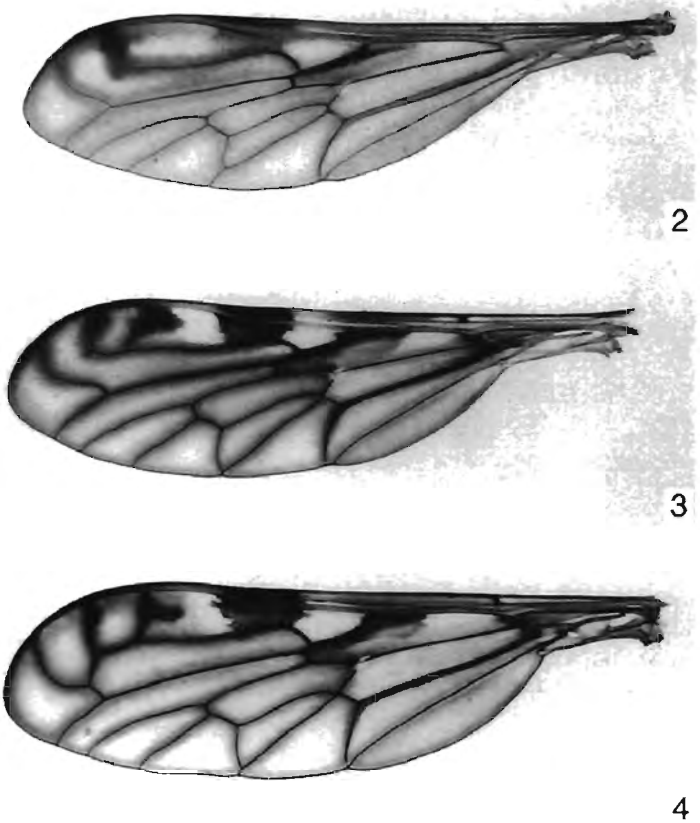
TAXONOMY

Genus *Leptynoma* Westwood, 1876

Leptynoma Westwood 1876: 517, *sensu* Stuckenberg 1996*b*: 251 (validation and division into subgenera).

The generic classification of South African Vermileonidae was revised by Stuckenberg (1996b). Several species formerly assigned to *Lampromyia* Macquart 1835, were transferred to a separate genus for which the name *Leptynoma* Westwood was retrieved from synonymy. The subgenera *Leptynoma s. str.* (type-species *Leptynoma sericea* Westwood 1876) and *Perianthomyia* Stuckenberg 1996b (type-species *Lampromyia maculata* Stuckenberg 1960) were established. *Lampromyia* was redefined and shown to comprise a clade of three eastern South African species and a larger, more diverse clade of palaearctic species (Stuckenberg 1998).

When the subgenera of *Leptynoma* were distinguished, it was noted that male specimens of *Leptynoma s. str.* are unique in an apomorphic form of the frons: the frons is peculiarly elongate and narrow, and tapers dorsally, at its apex being narrower than the width of the ocellar tubercle. The definition of this subgenus in couplet 4 of my key (Stuckenberg 1996*b*: 250) should be modified by insertion of 'male' before 'frons' in line 4. In the list of apomorphies used for cladistic analysis, no. 16 (op. cit.: 247) should similarly be modified by insertion of 'Male' at the beginning of the paragraph.



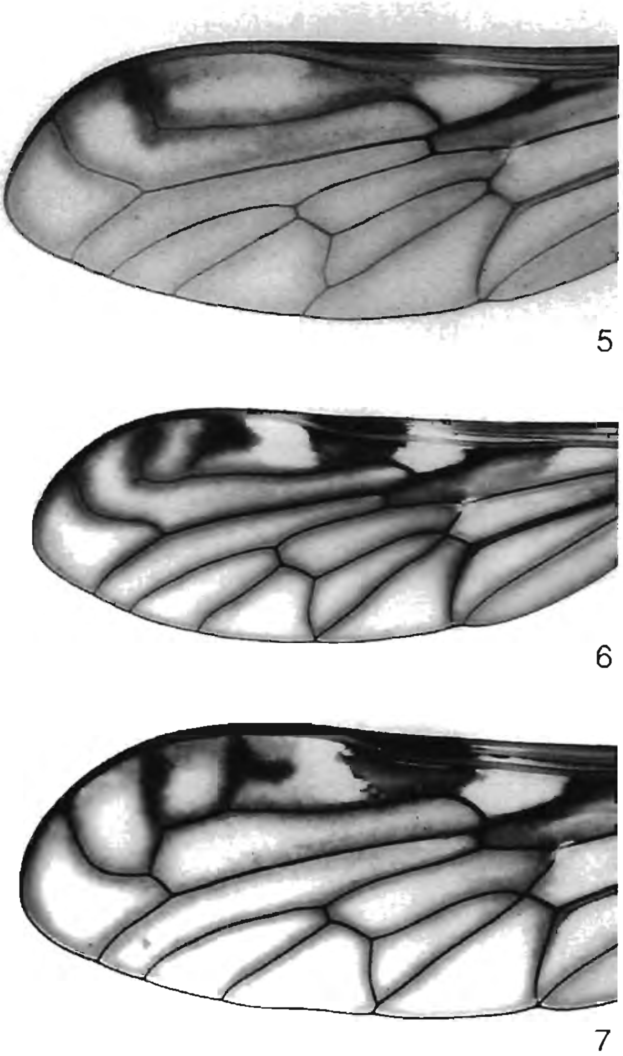
Figs 2–4. Wings of (2) *Leptynoma* (*L.*) species, showing patterning. 2. *L. appendiculata* (Bezzi). 3., (3) *L.* (*L.*) *namaquaensis* (Stuckenberg). , and (4.) *L.* (*L.*) *kirkspriggsi* sp. n., showing patterning.

The form of the female frons could not be fully described previously as flies of this sex were unknown for half of the species. Females of all species except the new Namibian one are now to hand. In *L.* (*L.*) *hessei* (Stuckenberg), *L.* (*L.*) *appendiculata* (Bezzi) and *L.* (*L.*) *namaquaensis* (Stuckenberg), the frons is approximately square or slightly longer than wide, with width about 20–22 % of greatest head width. In *sericea*, the lateral margins of the frons are slightly concave, and frons length varies from slightly shorter to slightly longer than frons width at midlength; its width is about 16 % of greatest head width.

A typographical error in my key to subgenera requires correction (Stuckenberg 1996*b*: 250, couplet 4): in the characterisation of *Perianthomyia*, the word 'lobout' should read 'lobe about'.

The fresh material of *hessei* and *appendiculata* recorded below reveals that antennal colouring more conveniently distinguishes these species than differences in form and proportions of antennal segments 8 and 9 previously specified. Couplet 3 of my key headed '*Males and females*' (op. cit.: 254) can be replaced by the following new couplet:

3. Antennal flagellum dark brown, distinctly darker than scape and pedicel .... **appendiculata** (Bezzi)
– Flagellum reddish-brown, not contrastingly darker than yellowish-brown scape and pedicel .... **hessei** (Stuckenberg)



Figs 5–7. Apical wing venation of (5) *Leptynoma* (*L.*) species. 5. *L. appendiculata* (Bezzi). , (6.) *L. (L.) namaquaensis* (Stuckenberg). , and (7.) *L. (L.) kirkspriggsi* sp. n. In Fig. 7 there is a proximally-directed, adventitious stump-vein on the supernumerary vein between R_{2+3} and the costa.

Leptynoma (Leptynoma) kirkspriggsi sp. n.

Figs 4, 7, 9–12

Etymology: Named in honour of Mr A. H. Kirk-Spriggs, Assistant Curator of Entomology at the National Museum of Namibia.

This species has dense silver pruinescence on the abdomen confined to the apical section (tergites 6–9), as in *hessei* and *namaquaensis*. It is easily recognised, and distinguished from all other Vermileonidae, by apomorphic modifications of the radial venation: R_{2+3} is divided apically into two veins that curve abruptly forwards to the costa (as if both R_2 and R_3 are primitively present), and a supernumerary crossvein extends between R_4 and the distal branch of R_{2+3}, vein R_4 being angled at the point of junction with this crossvein. In the spurious bifurcation of R_{2+3} this species resembles *namaquaensis*, with which it shares the following features: wing strongly patterned (compare Figs 3 and 4), hind legs boldly marked but fore and middle legs almost unicolorous, antenna relatively elongate (see Stuckenberg 1996*b*: Fig. 3), mesonotal vitta divided medially by a pale stripe, and abdomen strongly banded; in form of gonostyles and aedeagus, it also resembles *namaquaensis*.

Holotype ♂, 2♀ paratypes: NAMIBIA: Lüderitz [District]/ Rooiberg [Mountain]/ 27°38'S 16°28'E/ 22–24.ix.1997/ Kirk-Spriggs & Marais/ malaise trap sample. Genitalia of holotype in glycerine in microvial on pin. Holotype and one paratype in NMNW, one paratype in NMSA.

♂ (All specimens):

Head: Frons narrow, much longer than wide, narrowing towards ocelli; face and frons densely pruinose, face silvery, frons slightly greyish silver; antenna light brownish on scape and pedicel, becoming darker apically on compound segments 3–7, segments 8 and 9 dark brown; antennal form similar to *namaquaensis* but not quite as elongate, apical stylus segment slightly shorter than length of scape+pedicel. Proboscis blackish-brown, labrum reddish-brown; proboscis ratio variable: 2.5 (holotype), 3.3 and 2.1 (paratypes). Ocellar tubercle blackish-brown, thinly shining greyish pruinose.

Thorax: Mesonotum with dark brown median vitta which is divided along midline by a pale stripe, this vitta forking posteriorly into 2 tapering arms that extend backwards towards corners of scutellum, fork enclosing a dark brown median mark that extends to hind margin of mesonotum and is confluent with dark brown scutellar disc; mesonotum laterally with broad bands of sparse, shining, ashy-grey pruinescence with numerous, minute, dark, apruinose spots where hairs are inserted; median vitta demarcated laterally by narrow stripes of dense, slightly aureous, silvery pruinescence, these stripes broadening anteriorly between humeri and rounded apex of vitta; a conspicuous dark brown lateral mark on steeply declivous side of mesonotum behind transverse suture. Scutellum broadly bordered around margin with with dull yellowish-brown, sparsely silvery-pruinose on disc. Pleura brown, uniformly shining silvery pruinose with slight aureous tinge, similar pruinescence anteriorly and laterally on fore coxa.

Legs: Fore and middle legs, including coxae, uniformly yellowish-brown, tarsomeres 4 and 5 darkened, tibiae with recumbent, flattened, pale golden hairs; hind coxae and femur shining brownish, apical quarter of femur conspicuously dark brown; hind tibiae strongly banded, basal fifth dark brown (a very short terminal section pale), followed by a dull creamy band equal to about one-quarter of tibial length, remainder of tibia strongly brownish; hind tarsus weakly brown-tinged on tarsomeres 1 and 2, succeeding tarsomeres darker; hind tibia progressively much thickened apically over distal half (typical for this genus).

Wing: Membrane strongly patterned with brown as in Fig. 4, pale areas translucent greyish; in cell r_1 a strong brown mark confluent with stigma in apex of cell sc, contrasting pale areas present on either side, also pale markings in base of 1st basal cell and apically in subdivisions of cell r_{2+3}; most longitudinal veins bordered with brownish infuscation, leaving elongate, pale, less conspicuous areas centrally within cells; cell m_3 narrowly open in one paratype, closed with short stalk in holotype and other paratype. Modification of second radial vein as described above (Fig. 7); crossvein from apparent R_3 to R_4 consistently developed, but the following inconsistent venational abnormalities present: holotype left wing has basally-directed spurs on both apical branches of R_{2+3}, right wing has one spur on basal branch only (as in Fig. 7); one paratype has a spur on basal branch only (as in Fig. 7) on both wings, other paratype on left wing has spur on basal branch but its apex is abruptly bent anteriorly towards costa over short length, right wing without spurs on either branch of R_{2+3}.

Abdomen: Strongly banded due to transverse, pale, translucent yellowish-brown basal sections on each of tergites 1–5, these with thin, shifting silvery pruinescence, elsewhere these tergites shining dark brown; tergites 6–9 thickly silvery pruinose. Hypopygium (Figs 9–12) resembling *namaquaensis* (cf. Stuckenberg 1960, Figs 17, 21), especially in form of gonostyle as seen in dorsal view; aedeagus with numerous flat, triangular points on lateral extensions; differing from *namaquaensis* in form of gonostyle in posterior view, and in smaller ventral keel.

Size: Wing length: 8.6 mm (holotype), 9.3 mm (both paratypes); mesonotal length: 2.2 mm (holotype), 2.3 mm (both paratypes); proboscis length: 5.4 mm (holotype), 7.7 mm (paratype), 5.0 mm (paratype); body length excluding antennae: approximately 13.1 mm (both paratypes), not measurable on holotype due to arching of abdomen.

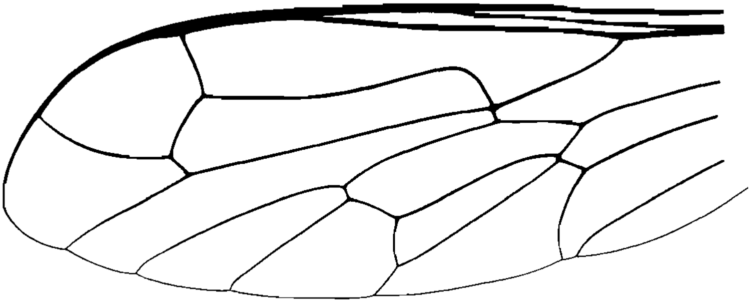
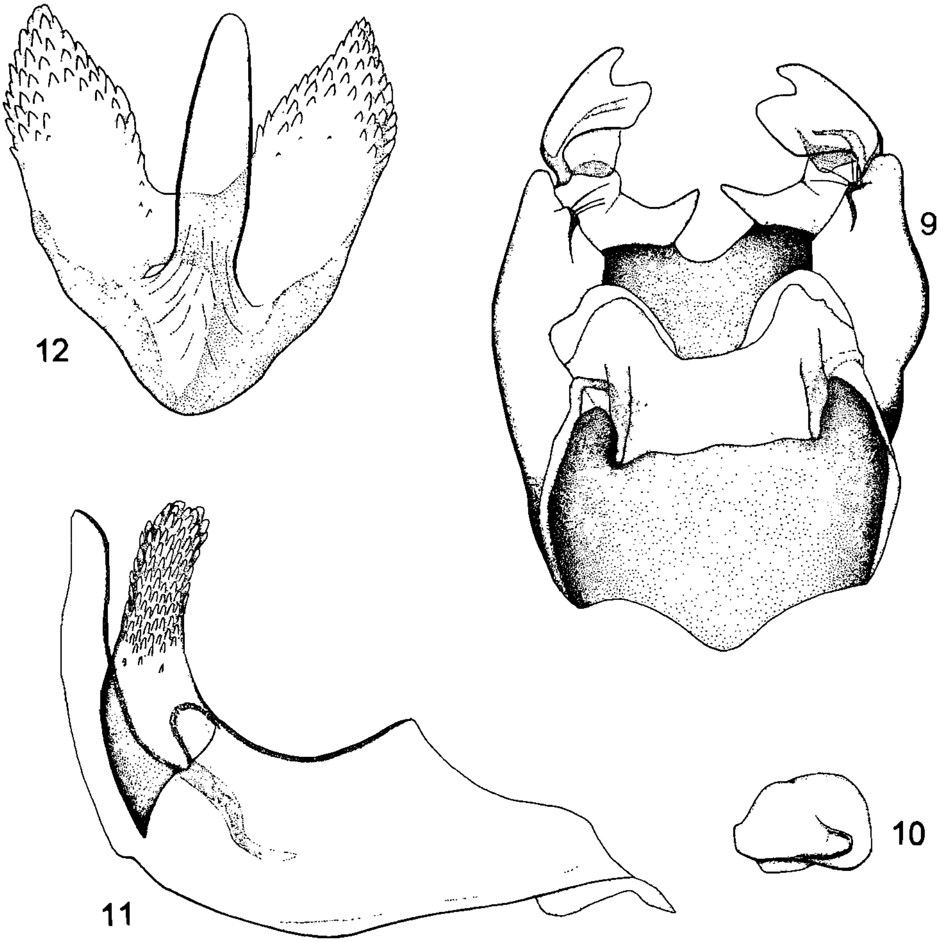


Fig. 8. Wing venation of atypical specimen of *Leptynoma* (*L.*) *appendiculata* (Bezzi), in which the short stump-vein at the angle on R_{2+3} (see Fig. 5) forms a crossvein connected with R_4 (see text).

RELATIONSHIPS

The resemblances noted above between *kirkspriggsi* and *namaquaensis* suggest that they are closely related. This is confirmed cladistically by the apomorphic secondary bifurcation of R_{2+3}. The cladogram given previously for *Leptynoma s. str.* (Stuckenberg 1996b, Fig. 13) is now modified to include *kirkspriggsi* (Fig. 13). Figs 5–7 show the probable progression of changes in R_{2+3}, starting with the condition in *appendiculata* which is the species basal to the clade with silvery pruinescence confined to the apex of the male abdomen. In *appendiculata* and *hessei*, R_{2+3} is angled apically, with a short stump-vein at the angle. In the *namaquaensis* + *kirkspriggsi* clade, R_{2+3} is bifurcate; contrary to my previous interpretation, this condition is now considered to have resulted from the formation of a spurious vein basal to the apical flexure of R_{2+3}. It seems less probable that a spurious vein should have grown out of the stump-vein and curved towards the costa, as the original course of R_{2+3} lies apically close to R_4 (see Fig. 5). A specimen of *appendiculata* collected on the Cape Peninsula (INHS, see below) is atypical in having the stump-vein at the angle continued to R_4 as a complete secondary crossvein in both wings (Fig. 8), indicating how the condition in *kirkspriggsi* (Fig. 7) could have evolved.



Figs 9–12. Male genitalia of *Leptynoma* (*L.*) *kirkspriggsi* sp. n. : (9. S) synsternite in dorsal view. , (10. R) right gonostyle in posterior view. , (11–112.—12) Aedeagus in lateral and posterior views.

The apomorphies establishing the cladogram in Fig. 13 are cited below as the italiciszed opening statement of each paragraph:

1. *Fork of R_4 and R_5 relatively short and wide, R_4 curving strongly forwards and meeting costa far anterior to wingtip, subparallel to apical part of R_{2+3}.* Only *sericea* retains a more plesiomorphic condition, with the fork deeper, and R_4 neither strongly curved forwards nor subparallel to the apical part of R_{2+3} (Stuckenberg 1996*b*, Fig. 14).
2. *Lateral arms of aedeagus with minute, flat, sessile points (see Fig. 11).* Present in all species except *sericea* (Stuckenberg 1960, Figs 21–24); they are absent also in *Perianthomyia*, *Lampromyia* and *Vermilynx*.
3. *Silvery pruinescence restricted to terminal tergites 6–9 in males.* In *sericea* and *appendiculata* the entire abdomen is silvery pruinose dorsally, and the same condition occurs in all species of *Perianthomyia*, so this is interpreted as the plesiomorphic state.
4. *R_{2+3} apically bifurcate as in Figs 6 and 7.* Only in *namaquaensis* and *kirkspriggsi*; a possible precursor condition is evidently shown by *appendiculata* (Fig. 5) and *hessei* (Stuckenberg 1996*b*, Fig. 16).

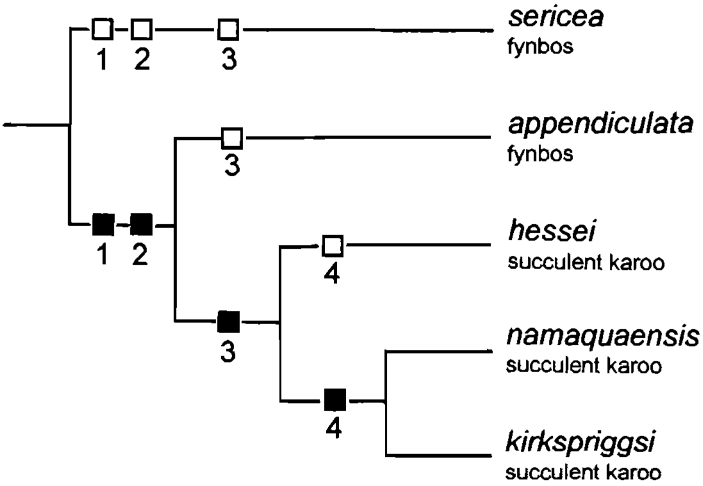


Fig. 13. Proposed cladogram for *Leptynoma* Westwood *s. str.*; solid squares represent apomorphies. Plant biomes inhabited by the individual species are stated.

NEW RECORDS

Vermilynx vansoni (Stuckenberg)

Lampromyia vansoni Stuckenberg 1965: 107
Vermilynx vansoni, Stuckenberg 1995*a*: 29–34.

1♂: NAMIBIA, from the Rooiberg mountain (see description of *kirkspriggsi* above for label data); in NMNW.

This is a particularly robust specimen; body black except for dull orange-brown on fore and middle femur and basal two-thirds of hind femur; scape and pedicel dull brownish, flagellum black; median mesonotal vitta bordered by narrow strips of golden pruinescence; scutellum entirely black; abdomen jet black; wings dark smoky-brown, unusual in this specimen in having contrasting pale greyish areas as follows: elongate and narrow in cell r_1 and discal cell; elongate and diffuse basally in 1st basal cell; subtriangular in cua_1; narrow, elongate, wider distally, in cup.

Measurements: wing 8.4 mm, proboscis 4.3 mm, mesonotum 2.2 mm.

Leptynoma (*Leptynoma*) *appendiculata* (Bezzi)

Lampromyia appendiculata Bezzi 1926: 301; Engel 1929: 172; Stuckenberg 1960: 238.
Leptynoma (*Leptynoma*) *appendiculata* (Bezzi), Stuckenberg 1996*b*: 255.

1♀: [SOUTH AFRICA] W. Cape/ Jacobsbaai, n. of/ Saldahna Bay/ 32°58'S, 17°54'E/ 7 Nov. 1996/ H.G.Robertson// in pitfall trap (SAMC). Teneral.
1♂: South Africa/ Cape Province:/ Kommetjie/ x-25-1972// J.G.Rozen/ R. McGinsy/ C.Thompson/Collectors. (INHS). Aberrant venation symmetrically developed on both wings (Fig. 8); a normal specimen was previously recorded from this locality (Stuckenberg 1996*b*: 255).
1♀: South Africa. W.Cape/ Prov.: Bokbaai, 15 km W/ Atlantis; 10-xi-1996, 0–100m/ coastal vegetated dunes/ 33°34'45"S, 18°18'45"E/ MEIrwin 29.x.1996. (INHS).
1♀: South Africa. W.Cape/ Prov. 3 km N Yzerfontein;/ 0–100 m. Malaise in/ coastal vegetated dunes/ 10-xi-1996/ 33°20'00"S, 18°09'00"E. (INHS).

Leptynoma (*Leptynoma*) *hessei* (Stuckenberg)

Lampromyia hessei Stuckenberg 1960: 233.
Leptynoma (*Leptynoma*) *hessei*, Stuckenberg 1996*b*: 256.

1♂ 2♀: South Africa. W.Cape/ Prov., Cederberg Mts.,/ 19km ENE Clanwilliam;/ 16-xi-1996. Malaise trap/ sandstone hillside, 400/ –500m/ 32°05'54"S, 19°03'06"E. (INHS).
1♂: Same data as above, except 14-xi-1996, 32°05'54"S, 19°03'56"E. (INHS).
2♂ 1♀: South Africa. W. Cape Prov./ 13.5 km ENE Clanwilliam, Pakhuis/ Pass: Malaise in stream bed/ 15-xi-1996. 900–1000 m/ 32°08'18"S, 19°01'14"E. 1♂ with same data except 16-xi-1996. (INHS).
3♂: South Africa. W.Cape Prov./ Cederberg Mts. Elizabethfontein/ 19 km NE Clanwilliam: shruby/ hillside: 15-xi-1996. 400–500 m/ 32°04'45"S, 19°03'29"E./ M.E.Irwin. (INHS).
1♀: South Africa. W.Cape Prov./ 12–13 km ENE Clanwilliam/ Pakhuis Pass, hillside stream/ bed: 18-xi-1996, 600–700 m/ 32°08'30"S, 19°01'30"E/ D.W.Webb. (INHS).

Leptynoma (*Leptynoma*) *namaquaensis* (Stuckenberg)

Lampromyia namaquaensis Stuckenberg 1960: 228.
Leptynoma (*Leptynoma*) *namaquaensis*, Stuckenberg 1996*b*: 256.

1♂ 2♀: South Africa., N.Cape/ Grootmis, 29.39'S 17.06'E/ (Valley behind church)/ 31.x.1996 M.W.Mansell. Collected as larvae, reared at Merrivale by BRS; emergence dates: ♂ 6.ix.1997, ♀ 23.ix.1997, ♀ 10.xi.1997. (NMSA).

Leptynoma (*Perianthomyia*) *phantasma* Stuckenberg

Leptynoma (*Leptynoma*) *phantasma* Stuckenberg 1996*b*: 260.

13♂ 1♀ : NAMIBIA, from the Rooiberg mountain (see description of *kirkspriggsi* above for label data); 7♂ in NMNW, 6♂ 1♀ in NMSA. The type locality of this species (at 27° 32'S, 16°11'E) is only about 30 km from the Rooiberg site.

1♂: Namibia. Fish River Canyon/ Park. 18 km E. Ai Ais. 480m./ malaise in dry wash in/ canyon draw; 19.xi.1996; M.E./ Irwin, E.L.Schlinger, D.K.Yeates/ 27°57'03"S, 17°32'35"E. (INHS).

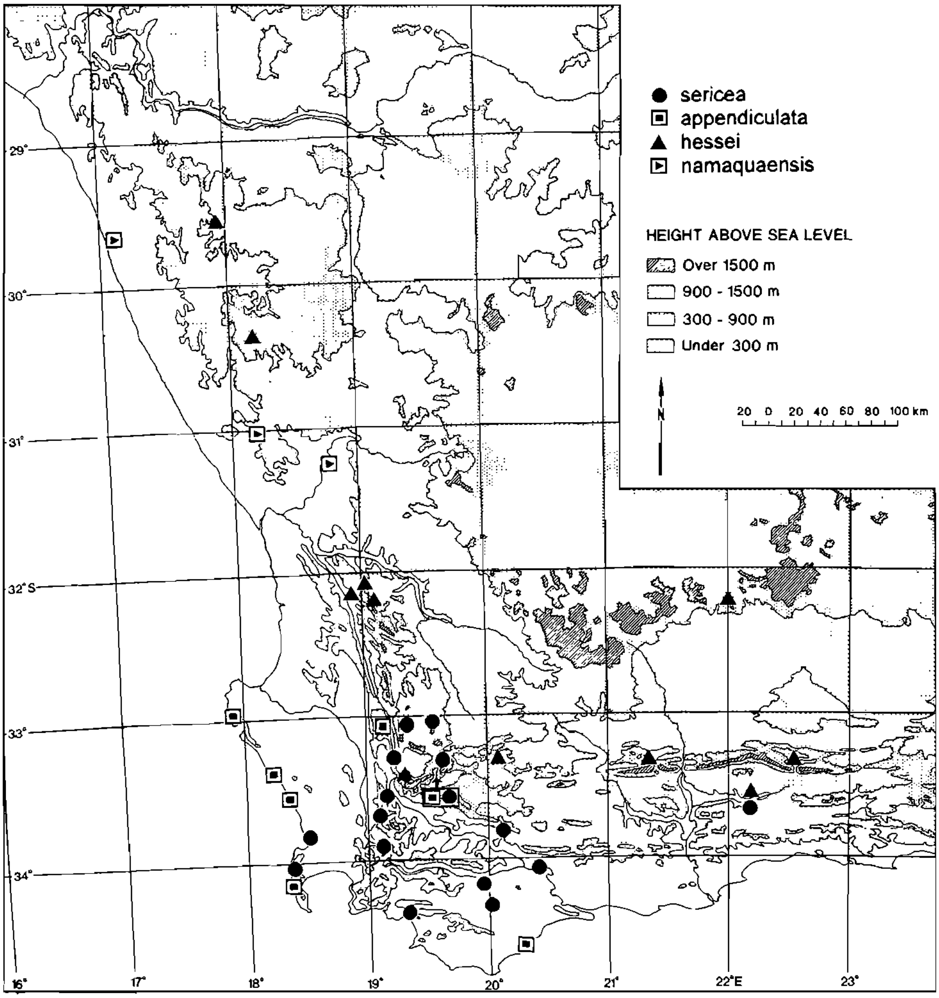

● sericea
▣ appendiculata
▲ hessei
⧐ namaquaensis
HEIGHT ABOVE SEA LEVEL
▨ Over 1500 m
☐ 900 - 1500 m
☐ 300 - 900 m
☐ Under 300 m
N
20 0 20 40 60 80 100 km
29°
30°
31°
32°S
33°
34°
16°
17°
18°
19°
20°
21°
22°E
23°

Fig. 14. Map showing the distribution of the four species of *Leptynoma* Westwood *s. str.* known in South Africa.

BIOGEOGRAPHY OF *LEPTYNOMA* S. STR.

The distribution of the four species of *Leptynoma s. str.* occurring in South Africa is mapped in Fig. 14. Plant biomes with which they appear to be associated are noted in the cladogram (Fig. 13). The cladistically basal species *sericea* and *appendiculata* occur in the Fynbos – the extensively documented shrubland which is the defining component of the *Flora Capensis*. This extraordinarily speciose biome is associated with sandy soils derived from the Fold Mountains made up of the Cape Supergroup formations in the south-western and southern Cape. Fynbos provides continuous habitat from coastal dunes to montane summits of 1200 m or higher, and these two species have a correspondingly wide altitudinal range.

The clade *hessei* + (*namaquaensis* + *kirkspriggsi*) is associated with another major plant biome – the Succulent Karoo, as defined ecologically by Rutherford & Westfall (1994) and described, *inter alia*, by Hilton-Taylor (1994). The Succulent Karoo comprises the Atlantic coastal strip and the western escarpment mountains, from the Lüderitz district of Namibia in the north, extending southwards to the Fold Mountains in the south-west Cape. It occupies an area receiving most of its rainfall in the winter months, and is restricted to those regions with pronounced summer aridity. The vegetation is low to dwarf, open to sparse succulent shrubland, with infrequent grasses, and mass flowering displays of annuals and geophytes in spring. The flora is remarkably large and highly endemic, with a diversity of succulent species '...unparalleled elsewhere in the world' (Hilton-Taylor 1994).

Of these three species, *hessei* has a wide distribution in interior parts of the winter-rainfall area seaward of the Great Escarpment. A detailed examination of collecting records shows it to occur at intermontane sites, in rainshadow zones, and on the drier ranges north of the Fold Mountains, as well as on mountainous parts of the escarpment in northern Namaqualand. These records indicate an association with Succulent Karoo, although *hessei* also occurs in some gorges incised through Fold Mountain ranges (eg. the Seweweekspoort) where mixed flora occurs, and has been found on the Cedarberg range where Fynbos is common.

The species-pair *namaquaensis* and *kirkspriggsi* occupy well-defined centres of endemicity within the Succulent Karoo, namely Namaqualand and the Gariep respectively. Seven subdivisions of this biome, and five centres of endemicity, are described and mapped by Hilton-Taylor (1994). Although *namaquaensis* is known from only three localities, my experience of this species in the field suggests that it is confined to the Namaqualand coastal plain and its low-lying hinterland below the western escarpment. This is a geologically young region, made up of deep Late Tertiary and Recent sands and gravels (Hendey 1983). The flora is arid-adapted, low in stature, dominated by succulents, and highly endemic.

The Gariep Centre (Fig. 1), transected by the Orange River valley, extends south from the Lüderitz district of Namibia, where the winter-rainfall zone peters out, to Steinkopf in northern Namaqualand, and from the Atlantic shore in the west to the escarpment mountains in the east (Hilton-Taylor 1994). It is geologically ancient, ecologically varied though entirely arid, and floristically diverse with an abundance of endemic species, but also with many links to the Namaqualand flora. To the north of Rosh Pinah in southernmost Namibia, a colourful profusion of flowering succulents in early spring gives the area a striking resemblance to Namaqualand. It was in that area that *kirkspriggsi* was found.

In considering the overall distribution of *Leptynoma s. str.*, the first matter to be addressed is how completely this is known. Both *sericea* and *hessei* might occur further eastwards, but the limit of the Succulent Karoo at about long. 23°E and changing taxonomic composition of the Fynbos with increasing proximity to the summer-rainfall zone, possibly constrain their distribution. Neither species was found in the Willowmore district (33°15'S, 23°30'E) by the late Dr H. Brauns, who lived there for many years; he was an excellent collector familiar with vermileonid larvae and flies. The subgenus has also never been collected inland of the Great Escarpment, where the Nama-Karoo Biome occurs (Rutherford & Westfall 1994). This vast region is very poorly collected; recent discoveries of undescribed species suggest that *Vermilynx* and *Leptynoma* subgenus *Perianthomyia* may be the only vermileonid taxa occurring there.

Factors limiting overall distribution are unlikely, in this case, to be the requirements of the immature stages. The larvae are predators of small arthropods caught in pitfall-traps made in fine, soft, dry, loose soil or sand in sheltered sites. In the open, largely treeless country frequented by *Leptynoma* species, suitable habitats could be available in a variety of situations: under ledges and overhanging rocks, in holes in banks, in caves, and perhaps just in shade under dense bushes in areas where rainfall is scanty. It is more likely that the range of *Leptynoma s. str.* is limited by constraints on the adult stage, imposed by associations the flies have with particular plant taxa. Specialisations for nectar-feeding at flowers are obvious: the proboscis is elongate, slender and capable of forward extension, and the narrow, petiolate wing-form is probably an adaptation for hovering to assist perching on flowers during feeding.

Mouthpart evolution in Southern African Vermileonidae has proceeded through a basal cladistic divergence and a subsequent sequence of developments in one of the resulting clades. The genus with the more primitive characters, *Vermipardus* Stuckenberg, has the shortest proboscis form and a unique labellar structure; it is the sister-group of all other afrotropical lineages and has had a separate history, being biogeographically distinctive and often associated with Afromontane Forest (Stuckenberg 1995*b*, 1997). The other genera form a monophyletic clade sharing a progressive tendency to proboscis elongation; the shorter proboscis of *Vermilynx* represents an intermediate stage, through which the long, forwardly-extensible condition in *Leptynoma* and *Lampromyia* evolved. Such a long proboscis form was evidently an evolutionary response to resources emerging during development of the Cape Flora.

Unfortunately there are hardly any records of flowers visited by vermileonid flies. The review of literature on pollination biology in the Fynbos by Whitehead, Giliomee & Rebelo (1987) cites records involving Diptera that are too generalised to be of much value. A colour-slide sent to me by Dr Hamish Robertson shows a female *L. sericea* feeding at flowers of *Lapeirousia corymbosa* (L.) Ker-Gawl (Iridaceae) at Kleinmond. The plant was identified by Dr J. Manning, who informs me that the flowers of this species are typical generalists with regular corolla and short tube. In the same general area I observed a male of *sericea* feeding at a species probably of the genus *Pelargonium* (Geraniaceae).

The study of pollination biology by Struck (1992) in the Goegap Nature Reserve at Springbok in Namaqualand, produced no records of vermileonid flies at flowers of selected common plant species. This reserve is the type-locality of *Vermilynx jasoni*

Stuckenberg (1996*a*), and *L. hessei* has been collected in the district (Stuckenberg 1996*b*). Probably these species are adapted to the flowers of small, less common plants not included by Struck in his survey.

Clear evidence of constraints on dispersal imposed by selective nectarivory has become available in a series of recent studies by Goldblatt, Manning & Bernhardt (1995), and Manning & Goldblatt (1996, 1997). In the first of these studies, on the pollination biology of *Lapeirousia* subgenus *Lapeirousia*, extreme adaptive radiation was found, resulting in the evolution of three pollination types: 1) flowers pollinated exclusively by large Nemestrinidae of the genus *Prosoeca* Schiner; 2) flowers pollinated exclusively by the large nemestrinid *Moegistorhynchus longirostris* (Wiedemann.); 3) flowers pollinated by an assortment of bees, bombyliid flies, and some Lepidoptera. It was observed that these nemestrinids also forage on flowers of other co-blooming plants, and sometimes indiscriminantly on *Lapeirousia* species where these are sympatric. Although floral specialisation evolved in guild-like relationships with these particular flies, the flies may be involved in more than one guild and are less co-adapted and dependant than the *Lapeirousia* species.

Manning & Goldblatt (1996) reported that a guild of 28 species of Iridaceae and Geraniaceae is pollinated exclusively by two species of Nemestrinidae: *Prosoeca peringueyi* Lichtwardt and *Prosoeca* sp. n. These are large flies with a long proboscis (up to 50 mm), which forage for nectar while hovering before flowers with the proboscis extended forwards. Floristic co-adaptations exist in the long floral tube (up to 70 mm), internal structure of the flowers to ensure pollen transfer to specific sites on the bodies of the flies, distinctive colouring (purple, crimson), and copious production of sucrose-rich nectar. The long floral tube excludes most other insects from the nectar, and ensures deep penetration by the flies and thereby contact with the anthers and stigmas. The distribution of the guild is restricted to Namaqualand and adjacent montane areas to the east, as well as to the Gariep. 'The combined ranges of the two nemestrinid species fall entirely within the main range of the plant species and accord almost exactly with the area within which two or more plant species occur.' (Manning & Goldblatt 1996). This is a clear demonstration of co-adaptation between flies and flowers as the dominant biogeographical determinant.

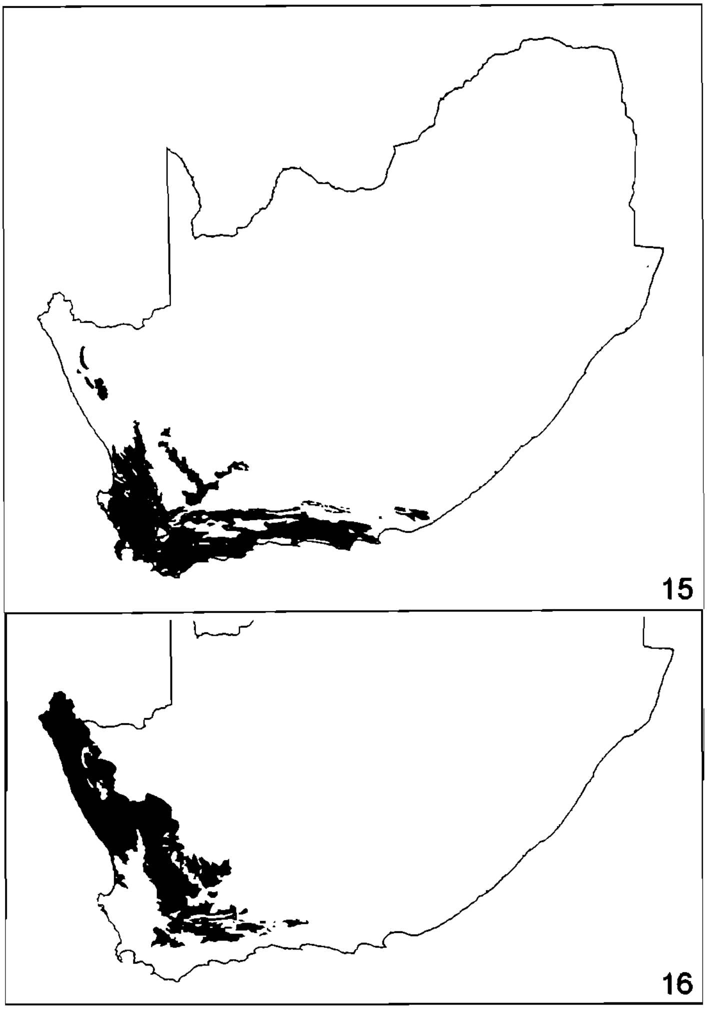
Further research (Manning & Goldblatt 1997) revealed that a guild of at least 20 species of Iridaceae, Geraniaceae and Orchidaceae is pollinated partly or exclusively by *Moegistorhynchus longirostris*; the crucial adaptation of this fly is the extraordinary length of its proboscis (up to 90 mm). It was also found that the horseflies *Philoliche gulosa* (Wiedemann.) and *Philoliche rostrata* (Linnaeus.) participate in the pollination of some guild members. Exceptional elongation of the labium (up to 40 mm) is a feature of these very big Tabanidae, although they retain the haematophagous habit. The authors show that the range of *M. longirostris* is confined to the main range of plant species in the guild. The two species of *Philoliche* are more widely distributed, and both range outside the limits of the guild; the anomalous eastern record of *gulosa* from Grahamstown is doubtful (Usher 1972).

It could be expected that diversification of the Fynbos, with its great taxonomic variety and profusion of flowers, would elicit co-adaptational responses among Diptera. Apart from striking examples such as the large nemestrinids and tabanids already mentioned, several interesting cases involving less conspicuous flies are known; these cases are significant because they involve morphological adaptations rare or unique in their families:

- *Arthroteles* Bezzi 1926 (Rhagionidae): the only rhagionid genus whose species have a long, slender proboscis (formed by elongation of the labium); several species occur in Fynbos of the SW Cape, and one on the KwaZulu-Natal Drakensberg Escarpment (Stuckenberg 1956); apparently the sister-group of the sympatric genus *Atherimorpha* White, whose species have the short, stout proboscis normal worldwide in rhagionid flies.
- *Peringueyomyina barnardi* Alexander 1921 (Tanyderidae): the only African representative of this archaic family, endemic to a small area of the SW Cape (Duxbury & Barraclough 1994); it is the only tanyderid with an elongate proboscis; the proboscis is formed by a ventral, tubular extension of the head capsule, bearing small mouthparts terminally; the flies occur in riparian sites along streams with stony beds in montane Fynbos.
- *Rhynchoheterotricha stuckenbergae* Freeman 1960 (Sciaridae): the only afrotropical sciarid with a very long proboscis, known from Fynbos on the Du Toit's Range and adjacent Hex River Range; as in the tanyderid, the proboscis is formed by tubular extension of the head capsule, and not elongation of the mouthparts (Freeman 1960); in a few non-African sciarids (eg. nearctic species of *Eugnoriste* Coquillet, and neotropical species of *Rhynchosciara* Rübsaamen) the mouthparts are elongate.
- *Forcipomyia* subgenus *Rhinohelea* De Meillon & Wirth 1979 (Ceratopogonidae): erected for two species of small midges with uniquely elongate mouthparts, occurring in Fynbos of the SW Cape; *F.* (*R.*) *briani* De Meillon & Wirth 1979, was collected from flowering *Erica* species (Ericaceae).

Many cases could be cited of Fynbos flies with less remarkable but nevertheless unusual mouthpart elongation. For example, the condition occurs in the genus *Phyto* Robineau-Desvoidy (Rhinophoridae), among closely related SW Cape species which show progressive stages in lengthening of the labium (Pape 1997).

The maps of biome distribution (Figs 15, 16) show that while Fynbos and Succulent Karoo contrast strongly in character, they are geographically contiguous in the SW Cape. The basal dichotomy in *Leptynoma s. str.* occurred in a Fynbos-inhabiting ancestor, leading to the *sericea* lineage and to its sister-lineage which subsequently diversified into other clades, with *appendiculata* retaining the association with Fynbos and cladistically basal to a radiation of three species in Succulent Karoo. The SW Cape probably provided the original locus for cladogenesis; the map (Fig. 14) shows that three species (*sericea*, *appendiculata* and *hessei*) include in their ranges a square of coordinates bounded by lat. 33° to 34°S and long. 19° to 20°E (Fig. 14). This is a region of ancient, complex topography formed by intersection of E–W and N–S series of Fold Mountains. Cladogenesis in the Succulent Karoo thus appears to be more recent. *L. hessei* has the widest distribution and ecological tolerance, and is basal to *namaquaensis* + *kirkspriggsi* whose ancestor adapted to increasingly arid conditions favouring succulence in the flora. Speciation followed or was coeval with differentiation of floral endemism in the Namaqualand and Gariep Centres.



Figs 15–16. Distribution of the Fynbos Biome (15) and the Succulent Karoo Biome (16) in South Africa. (From Low & Rebelo 1996, Figs 58 and 62.)

This hypothesis accords with current opinion concerning the age and relationships of these biomes. According to Cowling & Richardson (1995), the protofynbos expanded first during a drier phase of the Late Palaeogene *(ca.* 35 my). With climatic deterioration in the second half of the Miocene *(ca.* 16 my), there was a decline of forest and an increase in fynbos forms. By the Early Pliocene, Fynbos was extensively established in its present range and was predominant by the end of the Pliocene.

The numerous ideas regarding the origin of the Succulent Karoo are discussed by Hilton-Taylor (1987). Some authorities such as Goldblatt (1978) and Werger (1978) argued that the karoo flora, because of its highly specialised and endemic nature, evolved in Southern Africa over a very long period. Hilton-Taylor points out that high levels of endemism in the Succulent Karoo are confined to the species level, and that there is much speciation csurrently underway among succulent taxa and numerous morphological clines. He emphasised that '...many karoo species in the families Asteraceae, Scrophulariaceae and Selginaceae have close fynbos relatives'. Hilton-Taylor concludes as follows: 'Evidence to date indicates that only a few Cape taxa have their origins in the Karoo, whereas there are a number of studies indicating that many karoo taxa are derived from fynbos taxa.'

The pattern of cladogenesis in *Leptynoma s. str.* is congruent: it suggests that Fynbos is the older biome, and was the ancestral habitat of this subgenus. The physiognomic characteristics of Fynbos are well known to be considerably a consequence of the poor nutritional quality of soils derived from sandstones of the Cape Supergroup. Because the Fold Mountains are so old (folding completed by the Late Triassic), whatever angiosperm flora occupied them would have had to adapt to such soils. An early appearance of a flora with fynbos characteristics could thus be expected.

The ancestral form of the genus *Leptynoma s. lat.* probably existed by the Early Miocene, when a benign, warm, humid climate prevailed over South Africa, with forest, open woodland, grasses and protofynbos established (Deacon, Jury & Ellis 1992). With mid-Miocene climatic deterioration starting at about 16 my, *Leptynoma s. str.* and *Perianthomyia* could have diverged, the former in the Fynbos, the latter possibly in proto-Nama-Karoo, during the Late Miocene. With proliferation of the Fynbos, the basal dichotomy in *Leptynoma s. str.* evidently occurred in that biome; then would have followed emergence of the ancestor of the *hessei* + (*namaquaensis* + *kirkspriggsi*) clade, adapting from Fynbos into the evolving Succulent Karoo. With the onset of summer aridity in western South Africa from about the mid-Pliocene at 3.2 my (Deacon *et al.* 1992), cladogenesis occurred in response to the availability of new geographical terrain and succulent floristic resources in the Namaqualand pleistocene coastal plain; the ancestor of *namaquaensis* + *kirkspriggsi* extended its range from Namaqualand to north of the Orange River, and speciation as a consequence of vicariance followed as a relatively late development.

The case of *Leptynoma s. str.* appears to provide an illuminating paradigm, linking anthophily, cladogenesis and biogeography in the Fynbos and the Succulent Karoo. To validate this conclusively, it will be necessary to gather records of nectarivory by vermileonid flies in the biomes of the western Cape and the Gariep.

ACKNOWLEDGEMENTS

My sincere thanks are due to colleagues Dr Jason Londt and Dr David Barraclough for continuing support and for reviewing this paper. Mr Ashley Kirk-Spriggs of Windhoek (NMNW) is thanked for bringing the Rooiberg collection of vermileonids to my attention. I am grateful to Dr John Manning and Dr Craig Hilton-Taylor of the National Botanical Institute, Kirstenbosch, for sharing thoughts on plant-insect relationships and biome evolution. For the loan of specimens, I thank Dr Mike Irwin of the University of Illinois, and Dr Don Webb (INHS), both of Champaign, Illinois, as well as Dr Hamish Robertson of Cape Town (SAMC). The fine artwork and technical help of Ms Shayleen James and Ms Debbie Bellars are gratefully acknowledged.

REFERENCES

ALEXANDER, C. P. 1921. The crane-flies of South Africa in the South African Museum (Diptera, Tipulidae) Part 2. *Annals of the South African Museum* **18**: 181–230.

BEZZI, M. 1926. South African Rhagionidae (Diptera) in the South African Museum. *Annals of the South African Museum* **23**: 297–324.

COWLING R. & RICHARDSON, D. 1995. *Fynbos. South Africa's unique floral kingdom.* Vlaeberg: Fernwood Press. 156 pp. (reference, p.43).

DEACON, H. J., JURY, M. R. & ELLIS, F. 1992. Selective regimes and time. *In:* Cowling, R. M., (ed.), *The Ecology of Fynbos. Nutrients, Fire and Diversity.* Chapter 2, pp. 6–22. Cape Town: Oxford University Press. pp. 6–22

DE MEILLON, B. & WIRTH, W. W. 1979. Subsaharan Ceratopogonidae (Diptera) IV. *Rhinohelea*, a new subgenus of *Forcipomyia* from the south-west Cape Province, South Africa. *Annals of the Natal Museum* **23**: 881–886.

DUXBURY, K. J. & BARRACLOUGH, D. A. 1994. Rarely encountered Diptera families in southern Africa: an introductory conservation perspective. *Annals of the Natal Museum* **35**: 25–43.

ENGEL, E. O. 1929. A new species of *Lampromyia* (Dipt.) from South Africa. *Annals of the Transvaal Museum* **13**: 172–174.

FREEMAN, P. 1960. A new genus and species of Sciaridae (Diptera, Nematocera) from South Africa. *Annals of the Natal Museum* **15** (6): 75–77.

GOLDBLATT, P. 1978. An analysis of the flora of southern Africa: its characteristics, relationships and origins. *Annals of the Missouri Botanical Garden* **65**: 369–436.

GOLDBLATT, P., MANNING, J. C. & BERNHARDT, P. 1995. Pollination biology of *Lapeirousia* Subgenus *Lapeirousia* in southern Africa: floral divergence and adaptation for long-tongued fly pollination. *Annals of the Missouri Botanical Garden* **82**: 517–534.

HENDEY, Q. B. 1983. Cenozoic Geology and Palaeogeography of the Fynbos Region. *In:* Deacon, H. J., Hendey, Q. B. & Lambrechts, J. J. N., (eds), *Fynbos palaeoecology: A preliminary synthesis. South African National Scientific Programmes.* Report No. **75**: 35–60. Pretoria: CSIR.

HILTON-TAYLOR, C. 1987. Phytogeography and origins of the karoo flora. *In:* Cowling, R. M. & Roux, P. W., (eds), *The karoo biome: a preliminary synthesis.* Part 2 – *vegetation and history. South African National Scientific Programmes.* Report No. **142**: , Chapter 4. Pp.70–95. Pretoria: CSIR.

——— 1994. Western Cape Domain (Succulent Karoo). Republic of South Africa and Namibia. *In:* Davis, S. D., Heywood, V. H. & Hamilton, A. C., (eds), *Centres of Plant Diversity: A Guide and Strategy for their Conservation.* Vol. 1. *Europe, Africa, South West Asia and the Middle East.* Cambridge: WWF pp. 20–4217.

LOW, A. B. & REBELO, A. G. 1996. *Vegetation of South Africa, Lesotho and Swaziland*, 85 pp. (references on p. 58 and p. 62). Pretoria: Department of Environmental Affairs & Tourism.

MANNING, J. C. & GOLDBLATT, P. 1996.The *Prosoeca peringueyi* (Diptera: Nemestrinidae) pollination guild in southern Africa: long-tongued flies and their tubular flowers. *Annals of the Missouri Botanical Garden* **83**: 67–86.

——— 1997. The *Moegistorhynchus longirostris* (Diptera: Nemestrinidae) pollination guild: long-tubed flowers and a specialized long-proboscid fly pollination system in southern Africa. *Plant Systematics and Evolution* **206**: 51–69.

PAPE, T. 1997. Two new species of the *Phyto carinata* species-group (Diptera: Rhinophoridae). *Annals of the Natal Museum* **38**: 159–168.

RUTHERFORD, M. C. & WESTFALL, R. H. 1994. Biomes of southern Africa: an objective categorization. (2nd Edition.). *Memoirs of the Botanical Survey of South Africa*, **No. 63**: pp. 1–94.

STRUCK, M. 1992. Pollination ecology in the arid winter rainfall region of southern Africa: a case study. *Mitteilungen des Instituts für Allgemeine Botanik* **24**: 61–90.

STUCKENBERG, B. R. 1956. Notes on the Genus *Arthroteles* Bezzi, with descriptions of two new species (Diptera: Erinidae). *Annals of the Natal Museum* **13** (3): 313–335.

——— 1960. Diptera (Brachycera) Rhagionidae. *In:* Hanström, B., Brinck, P. & Rudebeck, G., (eds), *South African Animal Life* **7**: 216–308. Stockholm: Swedish Natural Science Research Council.

——— 1965. A new species of *Lampromyia* Macquart (Diptera: Rhagionidae) from the Richtersveld. *Journal of the Entomological Society of Southern Africa* **28**: 107–109.

——— 1995*a*. *Vermilynx*, a new genus for the wormlion fly *Lampromyia vansoni* Stuckenberg of the Richtersveld, southern Africa (Diptera: Vermileonidae). *African Entomology* **3**: 29–34.

——— 1995*b*. A taxonomic revision of *Vermipardus* Stuckenberg 1960, with descriptions of new species and notes on the biology and biogeography of the genus (Diptera: Vermileonidae). *Annals of the Natal Museum* **36**: 215–253.

——— 1996*a*. A new species of the wormlion genus *Vermilynx* Stuckenberg (Diptera: Vermileonidae) from Namaqualand, South Africa. *African Entomology* **4**: 197–202.

——— 1996*b*. A revised generic classification of the wormlion flies of Southern Africa previously placed in *Lampromyia* Macquart, with reinstatement of *Leptynoma* Westwood 1876, and descriptions of a new subgenus and two new species (Diptera, Vermileonidae). *Annals of the Natal Museum* **37**: 239–266.

——— 1997. Three new species of *Vermipardus* Stuckenberg, and a revised cladogram for the genus with novel biogeographical implications (Diptera: Vermileonidae). *Annals of the Natal Museum* **38**: 173–196.

——— 1998. A revision of the palaearctic species of *Lampromyia* Macquart (Diptera, Vermileonidae), with the description of a new Iberian species and a cladogram for the genus. *Bonner Zoologische Beiträge* **48**: 67–96.

USHER, P. J. 1972. A review of the South African horsefly fauna (Diptera: Tabanidae). *Annals of the Natal Museum* **21** (2): 459–507.

WERGER, M. J. A. 1978. The Karoo-Namib Region. *In:* Werger, M. J. A., (ed.), *Biogeography and ecology of Southern Africa.* Vol. 1, pp. 231–299. The Hague: Junk.

WHITEHEAD, V. B., GILIOMEE, J. H. & REBELO, A. G. 1987. Insect Pollination in the Cape Flora. *In:* Rebelo, A. G., (ed.), *A preliminary synthesis of pollination biology in the Cape Flora. South African National Scientific Programmes.* Report No. **141**. , Chapter 3. Pp. 52–82. Pretoria: CSIR. pp. 52–82.

WILLIAMSON, G. 1990.The Richtersveld, a treasure-trove of succulent plants. *Aloe* **27**: 34–39.